

COPULATORY BEHAVIOR OF DOWNY WOODPECKERS

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Study of the courtship of woodpeckers might be regarded as being in its infancy, as much remains to be done in showing how, in terms of evolution, patterns of courtship and pair bonds interrelate with feeding habits and a bird's total way of life. This point of view, discussed elsewhere in relation to the White-breasted Nuthatch (*Sitta carolinensis*) (Kilham, 1972a) and recently described by McKinney (1973) as ecoethology, is elaborated further in the final discussion of this report in relation to both Hairy (*Dendrocopos villosus*) and Downy (*D. pubescens*) Woodpeckers.

All aspects of the courtship of a species have to be studied in detail if ecoethology is to have meaning. This appears to be particularly true of the copulatory behavior of Downy Woodpeckers, which appears to be a unique performance and to have a special importance in promoting the pair bond as well as attachment to the nest site. That copulation in woodpeckers can have an important role beyond its ordinary one of reproduction has also been recognized by Short (1971).

Present studies were carried on mainly in Lyme, New Hampshire, between 1961 and 1973; 72 copulations were observed, mainly in three pairs whose nest sites were well-suited for observation.

Other accounts of the reproductive behavior of *D. pubescens* include those of Bent (1939), Staebler (1949), and Lawrence (1967), of which the latter two give descriptions of copulations. I have encountered no comprehensive account of the copulatory behavior, nor statement concerning the hover approach (described later) as being a unique performance. The main displays and vocalizations of Downy Woodpeckers are given in Kilham (1962).

DESCRIPTION OF COITION

Invitation pose of female.—When ready for copulation a female Downy Woodpecker may fly to the male, perching crosswise or occasionally lengthwise on a horizontal limb (Fig. 1), raise up on her legs with, to shorten a description by Lawrence (1967), "her tail pointing straight out, her head up and tilted backward, her . . . breast thrown out, her wings slightly dropped and motionless." This performance results in an outline more like that of some passerine species, a fact also noted by Steinfatt (1937) for the female of the Great Spotted Woodpecker (*D. major*).

Hover approach of male.—The male landed on the back of the female following a hovering approach in all of the observed copulations. An example illustrating the main features of these hovers is as follows:



FIG. 1. Copulatory behavior of the Downy Woodpecker showing the flight and hover of the male as well as the invitation pose of the female.

On 6 May 1971 Male B was resting on a horizontal branch close to the nest hole when the female flew to him. He immediately moved until he was 30 cm away from her and facing in an opposite direction, then launched himself in a slow, hovering flight, turning in the air when in a position about 60 cm below and 1.3 m behind his mate (Fig. 1). From here, still hovering and almost stationary, he slowly rose until he was slightly above her and landed on her lower back. Copulation then followed, the hover preceding it having taken about 2 seconds.

Configuration of branches and tree trunks where the female took her invitational pose might alter the pattern of the approach as well as of copulation. A feature was that the male often moved away from his mate when she flew to him, sometimes moving as much as 75 cm, as though he needed room to maneuver in launching his aerial approach. Lawrence (1967), in a description of the hover, states that the male "left his perch and on rapidly beating wings hovered above (the female) for about 5 seconds." In the approaches I have witnessed the male reached a point above the female only at the very end of his performance, and hovering lasted only 2 seconds.

Two aspects of the hover are worthy of emphasis. One is that it possibly is unique for *D. pubescens*, as I have not encountered description of it for

any other woodpecker species, including the similar-sized European Lesser Spotted Woodpecker (*D. minor*). Hovering is found in other groups of birds. Hinde (1954), for example, describing it in detail for the Green Finch (*Chloris chloris*). The second aspect of the hover is that the male Downy Woodpecker acts almost as if repelled by the female. Thus, as I saw repeatedly, if the female flew close to him to assume the copulation pose, he would move away rather than toward her. It is conceivable from this point of view that the hover flight evolved from this initial repulsion. By the deliberate hover and approach from the rear, taking appreciable time, a male may be able to overcome his initial aversion to physical contact.

It is curious that Staebler (1949), who describes eight copulations of *D. pubescens*, makes no mention of the hover approach. One wonders, therefore, whether he failed to notice it or whether this behavior occurs in some parts of the species range and not others. Staebler mentions one male as fluttering on the back of a female, but such fluttering can be seen with many species of woodpeckers (as well as other birds) when a male, off balance, seeks to stabilize himself.

Coition.—Once mounted on the back of the female, the male Downy, like the males of other species of woodpeckers (Lawrence, 1967; Blume, 1963; Kilham, 1959, 1966a) falls gradually to the left. During this time his tail is moved under that of the female and at the time of cloacal contact is turned forward to lie along her right side. The male meanwhile holds his balance by spreading both wings. His right wing may lie across the lower back and tail of his mate while his left one rests against the branch where she is perching. The period of close contact is held for a seemingly long time. I have timed it as ranging from 10 to 16 seconds both with a wrist- and a stopwatch: Lawrence (1967) gives timings of 14 and 18 seconds and Staebler (1949) of 12–15 seconds. The male, while thus more or less inverted, is usually looking upward and moving his head about. This is in contrast to the Hairy Woodpecker (*D. villosus*) which, as Lawrence (1967) has also noted, may lie so both male and female have their heads nearly in parallel and are looking in the same direction.

Abortive coitition.—At times the male may mount the female as in full copulation, but once mounted, both birds fall away within a few seconds, suggesting either one or both is not in sufficient readiness. In 1971 I saw seven abortive copulations in the same period as 24 full copulations and in 1972 five abortive copulations to 15 full copulations.

CIRCUMSTANCES ATTENDING COPULATION

In studying Pair B, I visited the nest stub every day except one between 6 May and 22 June 1971, spending on an average an hour in the morning

and a half hour in the afternoon on week days and almost twice this time on weekends. Trees in the swamp were low and bare of obstructing foliage throughout much of May. Details of circumstances attending copulations were as follows:

Location.—All of the 24 copulations noted for the swamp pair took place within 7 m, and usually less, of the nest hole, which was 10 m above the swamp. Most of them, i.e. 17 of the 24, occurred on a favored "copulation" branch that extended within 9 m of the entrance. The male, spent much of his time within a short flying distance of the nest stub, and I had no evidence of copulatory activity occurring elsewhere in periods of observation. All of the 72 copulations noted for a total of 8 pairs of *D. pubescens* took place close to the nest, as is also described by Lawrence (1967) and Staebler (1949). This would seem to be a feature of the copulatory behavior of this species, even though I might have missed some copulations taking place elsewhere. I have not observed any such constant relation in *D. villosus* (Kilham, 1966a and MS) and Short (1971) notes that only a few of the copulations he observed in Nuttall's (*D. nuttalli*) and Ladder-backed (*D. scalaris*) woodpeckers occurred in the proximity of nest sites. Pynnönen (1939), on the other hand, states that most of the copulations of the Greater Spotted Woodpecker (*D. major*) take place near the nest, where the two sexes meet most often. He also noted that copulations often took place on a definite branch.

Time of day and frequency.—The copulations of Pair B were noted at all hours from 06:30, which was within 10 minutes of the time the male emerged from roosting, until 17:40: 13 of the 24 were in morning hours, a time of greater activity also noted by Pynnönen (1939) for *D. major*. The greatest frequency was at the time of egg-laying. On 11 May, for example, copulation at 10:45 was followed by a second one only 2 minutes later, and a third one, following an abortive attempt, at 11:10. This spate of copulations in a 25-minute period was exceeded 4 days later, on 15 May, when three copulations took place in the 17 minutes between 06:48 and 07:05. On the following day copulation at 07:32 was followed by another 2 minutes later. I timed these two as lasting 14 and 10 seconds respectively. Considering that on most days I was only by the nest at hour and half hour periods, the total number of copulations per day must have been well beyond the recorded numbers. Pynnönen (1939) states that *D. major* may copulate six times a day in the egg-laying period.

Invitation to copulation.—Copulations may be initiated by either the male or the female. In many cases the two birds seemed in equal readiness, the precipitating circumstance being that both were by the nest at the same time. Between copulations, or several of them occurring close together, only a

single bird, usually the male, remained near the nest. The range of circumstances preceding copulations were as follows:

(i) In the first days of the copulation period (6-8 May), MB would be excavating while his mate, who did almost none of the work, was away. I seldom saw FB except when she came for copulation. If her mate was within the nest hole, she would fly to it directly, then fly to the copulation branch to take her invitation pose when he looked out. On occasions when MB was already out of the hole, at times preening in leisurely fashion on the copulation branch, the female would still fly to the hole before coming to him. This initial flight to the nest is also described by Shuster (1936) for the Lesser Spotted Woodpecker. He considered it an important link in the chain of copulatory behavior and, as in the case of *D. pubescens*, this aspect of the behavior of the female suggests that copulatory behavior, among other purposes, serves to strengthen emotional attachment to both nest and mate.

(ii) Female B was apparently laying eggs from 11 to 18 May, hence she was by the nest hole more than previously. She had been able to enter the hole readily before this time, but during this period had difficulty. She would bow in and out of the hole, on occasions 12 to 15 times, before being able to force her way in, possibly due to an increase in body size when carrying an egg. She also spent much time resting below the hole. When her mate, who always stayed away when she was by the nest, flew in and alighted on the copulation branch, she would then fly to him to copulate. It thus seems that initiation of copulation might be by either sex, according to the phase of nesting.

(iii) Either bird might drum in seeking copulation as also noted by Staebler (1949). On 8 May FB drummed for 3 minutes about 20 m from the nest stub, then she flew to the hole and from there to the preferred branch for copulation. On 16 May, after finishing the nest excavation and before the onset of incubation, the male spent much time idling by the nest, as he often did in the interim. After 50 minutes of this he drummed for several minutes, at 10:25 and again at 10:36. His mate flew in after the second drumming and copulation followed. A similar sequence had occurred the day previously, shortly after the male emerged from roosting at 06:45. During his periods of idling the male gave occasional "whinnies." As noted for other pairs, "whinnies" are given by both sexes, but especially by the male during the period of copulations, although not associated with them as directly as the drummings.

Behavior following copulation.—There was no set behavior following copulation. In the period 6-8 May the male often returned to the hole to continue excavating and in the period 11-18 May, that of egg-laying, the female might fly to rest below the entrance. On two occasions she remained on the copu-

lation branch, still perching crosswise, and the male returned within 2 minutes for a second copulation. At other times the female moved to a tree trunk nearby. I twice saw the male hovering close to her as she shifted about the trunk. Either after such an episode or soon after copulation, the female might fly off with the male in pursuit.

Lawrence (1967) also mentions this pursuit flight. She describes the female as inviting the male to follow. Another interpretation, suggested by the behavior of Pair B, was that in some instances the female might be satiated while the male still had an urge to copulate. He might then hover seeking further contact with the female. When she failed to respond, the male may have been expressing instincts in the pursuit flight. In this respect the pursuit flights of the White-breasted Nuthatch (*Sitta carolinensis*) (Kilham, 1972a) appear, to be similar in nature to those of *D. pubescens*.

Copulatory activity during incubation.—Incubation in Pair B began on 18 May, and although I saw no copulations on that day, I did see one each day on the 19th, 21st, and 22nd. The last one was thus on the fifth day of incubation, after which copulatory behavior was sporadic and fragmentary. On 25 May the male drummed when coming to the nest then alighted on the copulation branch. His mate, meanwhile, flew out from the nest hole and took an invitation pose on the branch, but flew off before he had a chance to hover. On the following day, the ninth of incubation, the male chased her in a pursuit flight after a roughly similar episode. The last of the fragmentary type of behavior was seen on 29 May, close to the time of hatching.

Lawrence (1967) states that copulatory behavior declines first in the female. This was not evident with Pair B, however, as the partners appeared to lose interest more or less simultaneously. Pynnönen (1939) similarly noted in *D. major* that once incubation had begun, the male at one time and the female at another might be ready for copulation when its mate was not. He also found, as I did for *D. pubescens*, that the last full copulations of *D. major* and *D. minor* took place five days after incubation had begun.

OTHER ASPECTS OF COPULATORY BEHAVIOR

Copulation with an intruder.—On the morning of 9 May FB fell from a tree in spasm, apparently due to retention of an egg as described elsewhere (Kilham, 1972b). I took her home before returning her, still essentially helpless, to the swamp an hour later. I saw no more of her until 11 May. By the afternoon of the day she disappeared (9 May) a female (NF) with very different head markings had arrived by the nest. A feature of her behavior during the two days of her stay was that she began an excavation of her own in a stub 7 m from the nest and worked at it periodically and without interference from male MB. NF hitched up his nest stub twice while

I was watching. Each time MB attacked and drove her away. He was otherwise tolerant of her presence. On 9 May, not long after being chased away, NF took an invitation pose on a nearby branch and I saw MB hover. Copulation probably followed, but I was not in a position to see well. On the next day, at 10:45, I watched a full copulation under much the same circumstances. NF remained in position after the male had left. He returned and mounted her again in an abortive copulation. NF then circled his nest stub, but when within 20 cm of the hole, the male not only attacked but also pursued her in a long flight. I saw no more of NF on following days when FB had returned.

Lawrence (1967) gives description of a somewhat similar episode. In her case the females of two adjacent pairs were laying eggs when one of them was killed. The still-mated female had to pass through the territory of the newly unmated male to reach a feeding station, and while doing so she stopped on a branch near his nest stub, took an invitation pose, and copulation followed. A case of promiscuity is also mentioned by Staebler (1949).

Notably in Pair B, although MB was willing to copulate with the new female, he was quick to drive her away from his nest and hence did not accept her as a mate. This jealous attachment to the nest appears to illustrate the crucialness of the cavity to the pair bond of *D. pubescens*. The fact that all or nearly all copulations took place in its vicinity may well have served to strengthen this attachment.

The new female, NF, was evidently in search of a mate in association with a nest hole. Unable to visit the hole already constructed, she had an immediate urge to set about excavating another close by. The willingness of the male to copulate with the intruder, in this case as in that of Lawrence, is understandable in view of the male's peak of sexual readiness.

Loss of nest and effect on copulations.—In 1972 pair B excavated a nest cavity 60 m from where they had nested the year before. I saw a first abortive copulation on 6 May and a full copulation at 16:45 on the following day. MB did almost all of the excavating which he largely completed by 11 May. Although I saw 4 copulations between 13 and 17 May, MB, contrary to his behavior of the year before, did not remain by the nest hole. It was an unusually cold spring and it seemed probable that a general lack of insect life gave little inducement to start nesting. His absence left the hole unguarded, and a pair of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) that he had driven away repeatedly on other days, took over the nest cavity. They quickly enlarged the entrance on 18 May until it was no longer suitable for the Downy Woodpeckers. By the next day MB was exceedingly active in looking for a new nest site. In spite of the absence of a definite nest site, copulatory behavior of MB and FB continued. At 07:30, for example, MB had started

a trial excavation in stub No. 1 when FB flew to him and copulation followed. By 09:47 MB had started trial excavation in stub No. 2, when his mate flew to him as before and copulations followed on a nearby branch. It was apparent from these episodes that a completed nest cavity was not needed for copulation to occur, and I was also to observe such behavior in a following year. MB tried five different sites before finally selecting one on 19 May. He worked incredibly hard on 19 and 20 May, seeming to complete most of the work those two days, with little time taken off for feeding. In spite of this pace, copulation continued. Each time, FB initiated the copulation by flying to a branch close to the excavation and he then flew to her. The last copulations seen were on 24 May.

Early copulatory behavior.—Although the period of daily copulations does not begin until a nest is nearing completion, several observations made in 1973 indicated that isolated copulations can occur at the start of excavations. On 2 May, for example, I found Male C with just his head in a hole recently begun: and later abandoned his mate flew to a branch nearby and a full copulation followed. In 1968 I had noted a similar situation, with two copulations in 4 minutes on 27 April by a site later abandoned by the pair. A third example of early copulation was with Pair D. On 6 May 1973 Male D was still working on his outside nest hole when his mate came near and the two had an abortive copulation. My wife and I watched the nest for 2 to 4 hours daily for the next 2 weeks. We saw no further copulations until 10 May, and then witnessed them almost daily, with 21 the total reached by 21 May.

EXPERIENCE WITH A HAND-RAISED PAIR

I raised a brood of Downy Woodpeckers in an aviary in 1959, and in the following year a pair of them excavated a nest hole. On 28 April the female started taking invitation poses, but the male showed little sign of readiness until 1 May when he mounted in an effort at copulation. He did not use the hover approach and as he mounted he fell off to the right. On 5 May he again copulated in similar fashion. None of the five eggs subsequently incubated by both Woodpeckers was fertile.

From this one might conclude that the male *D. pubescens* may not be sexually mature in his first nesting season, a situation also noted for *D. villosus* (Kilham, 1966a). If the aviary Downy was indeed sexually immature, he may not have yet acquired complete copulatory behavior, including the hover approach and falling to the left. Lawrence (1967) noted that "the act (coition) requires no little skill on the part of the male. Young and inexperienced males often show that the movements are not altogether innate but are to some extent learned. Some individuals at times display distinct

TABLE 1

COMPARATIVE BREEDING AND COPULATORY BEHAVIOR, BASED ON 72 COPULATIONS NOTED FOR THE DOWNY AND ON 49 FOR THE HAIRY WOODPECKER IN NEW HAMPSHIRE

Activities of Paired Males (M) and Females (F)	<i>D. pubescens</i>	<i>D. villosus</i>
Vocalizations on meeting—	“Chirr”	“Joick, joick” “tewk, tewk”
character—	Harsh	Exuberant
Travel together in feeding	Seldom; well separated	Frequent (for a part of each day)
Supplanting attacks M on F	Frequent	Infrequent (away from feeders)
Tapping by potential nest hole	Relatively seldom	Frequent
Onset copulatory behavior	May	February-March
Copulations	Duration	13-16 seconds
	Character	M first moves away, then flies as to approach F from rear; hovers
	Location	Close to nest excavation (within 15 m)
		6-10 seconds
		M ascends trunk and moves out along branch directly to F.
		No flight or hover
		Close to nest 22 times, away from nest 27 times

bewilderment and hesitation . . .”. Along these lines she describes an inexperienced male that hopped along a branch to the female, with no hover, and “twice . . . hesitated, recoiled, then again advanced, as if something in the situation were radically wrong. Finally he reached her, mounted, tramped on her back, still hesitating, then swung himself under her tail—but lost his grip and fell off.” Both birds on separating, resorted to displacement pecking.

Both Lawrence’s observations and my own thus support a concept that the complete copulatory behavior, while basically innate, is something the male has to learn as well.

DISCUSSION

Although the courtship and copulatory behavior of Hairy Woodpeckers has been described in Kilham (1966a), many additional observations made since that then have gone into the summaries shown in Table 1. The breeding activities listed there for *D. villosus* are all suggestive of a close pair bond. To a human observer a pair of that species appears to enjoy each other’s company with relatively little repulsion to physical contact, as indicated by copulatory activity beginning in February, and to have a pair bond tied in

with the nest site but not to the extent seen in *D. pubescens*. In almost every activity listed in Table 1, Downies differ from Hairy Woodpeckers. One's impression of *D. pubescens* is of a mild repulsion operative between the members of a pair, in the female possibly through fear of the male and in the male through his aggressiveness in supplanting attacks. The nest cavity, chiefly excavated by the male as also noted by Lawrence (1967), is the center of the copulatory activity which, in being the chief and almost the only form of courtship, and thus serves a dual function.

The Heinroths (1958) have stated that "many . . . woodpeckers are not particularly fond of their mates." While this statement does not apply to such species as the Hairy, the Pileated (*Dryocopos pileatus*), and the Crimson-crested (*Campyphilus melanoleucos*) Woodpeckers (Kilham, 1959a, 1966a, 1972c), to cite a few examples, it does appear to apply to the Black-backed (*Picoides arcticus*) (Kilham, 1966b), Downy, and, to judge from descriptions given by Bock (1970), Lewis' (*Asyndesmus lewis*) Woodpeckers.

One may wonder why the breeding and courtship behavior of two similar plumaged, sympatric species such as *D. pubescens* and *D. villosus*, should be so remarkably different. The matter of maintaining reproductive isolation may be only a partial answer. Natural selection, according to Mayr (1963), is always a compromise, and from this point of view the breeding behavior of a species is tied in with its total economy. This basic difference between Downy and Hairy Woodpeckers relates to bill size and feeding habits. From observations made in New Hampshire, it has seemed to me that *D. villosus*, in having evolved sexual differences in feeding behavior (Kilham, 1965), as well as a strong bill to dig out larger wood-boring larvae, can survive well in winter on its breeding territory. The ample food supply gives Hairy Woodpeckers a margin of leisure in winter that can be devoted to courtship. In this respect, as discussed elsewhere (Kilham, 1972a), they resemble the sympatric White-breasted Nuthatches, which also begin breeding behavior in January and February.

These situations are very different for *D. pubescens*. Its winter food supply, at least in Lyme, New Hampshire, appears to be marginal. Individuals seldom remain on their breeding territories in winter, as Lawrence (1967) has also noted for Canada. In some winters a number concentrate where food is locally prevalent, as on paper birches (*Betula papyrifera*) infested with the coccid *Xylococcus betulae* (Kilham, 1970). Even there, Downy Woodpeckers appears to need all daylight hours to find enough prey to survive. In a more closely competitive situation, males make relatively frequent supplanting attacks on females. This leads to a spacing out of the sexes, with males feeding on the upper part of the birches. While this leads to a more efficient

utilization of resources, the aggressiveness of the males and the need to feed steadily all day do not favor any early onset of breeding behavior. The margin of leisure needed for full courtship depends on a relatively abundant food supply. For *D. pubescens* this does not come until May with the emergence of new populations of insects that it can obtain by gleaning. By this time the pair has formed and a nest site has been selected and largely excavated by the male. Up until this time the members of a pair continue to spend a minimum of time together, as in winter. This situation changes when the completion of the nest hole coincides with the onset of warmer weather, as it usually does. Copulatory behavior then begins and serves, in addition to its strictly reproductive function, as the main form of courtship.

SUMMARY AND CONCLUSIONS

Downy Woodpeckers appear to have a unique form of copulatory behavior in which the male may first move away from a soliciting female, then fly to approach her from the rear in a hovering flight.

Successful copulations last 13–16 seconds, which is relatively long in comparison with those of the related, sympatric Hairy Woodpecker.

Copulations may take place many times a day, over a 2-week period that may extend from the end of nest excavation up to the fifth day of incubation. These may be preceded by a few copulations at the very beginning of an excavation.

All of the 72 copulations observed at this time took place in the vicinity of the nest cavity, attachment to which appears to be tied in closely with the pair bond in *D. pubescens*.

Several unusual incidents were noted. In one of these a female was absent for 2 days, and an intruder female immediately took her place. Although the intruder copulated with the male, the male would not allow her to come close to the nest.

In a second incident, the nest cavity was taken over by sapsuckers at the beginning of the copulatory period. The copulations of the pair of Downies continued nonetheless, the female flying to wherever the male was excavating in his varied search for a new nesting site.

The members of pairs of *D. pubescens* are relatively antagonistic to each other during much of the early breeding season, with almost none of the intimate vocalizations and displays observable in the courtship of *D. villosus*. Under these circumstances copulations appear to serve as a comparatively important form of courtship as well as having a strictly reproductive function.

In both *D. pubescens* and *D. villosus*, patterns of courtship appear to have evolved in close relation to the feeding behavior of winter and spring months; differences in the total economy of each species accounting for differences, among other things, of the nature of their pair bonds.

ACKNOWLEDGMENT

I have been much aided in these studies by my wife, Jane Kilham, for redrawing the field sketch shown in Figure 1 and in helping to watch at the nests.

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NEW HAMPSHIRE 03755. ACCEPTED 14 SEPTEMBER 1973.